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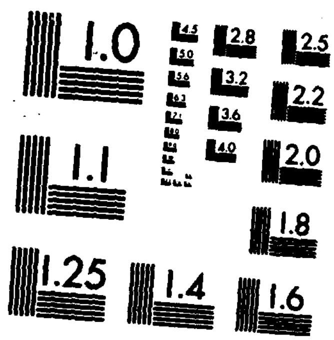

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Biological Investigations of Adaptive Networks: Neuronal Control of Conditioned Responding

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Neurobiological investigations of adaptive neural networks were conducted using the classically conditioned nictitating membrane response (NM CR) of rabbit, a widely used model system for studies of learning. One experimental approach involved recording from single brain neurons from awake, behaving animals for the purpose of determining the loci and characteristics of neurons with activity correlated with the NM CR or its inhibition. A second approach involved the use of discrete brain lesions that selectively eliminate the NM CR while at the same time sparing the basic reflex pathway. A third approach employed fiber-tracing anatomical techniques designed to clarify the interconnectivity among brain regions essential for the NM CR. These regions include discrete protions of the cerebellum and brain stem. Information from physiological studies has been incorporated into mathematical models of learning used by adaptive network researchers, and anatomical findings have guided the development of related neuronal models. Keywords:

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Biological Investigations of Adaptive Networks: Neuronal Control of Conditioned Responding

Dr. John W. Moore, Ph.D., Principal Investigator

University of Massachusetts, Amherst

I Summary

Neurobiological investigations of adaptive neural networks were conducted using the classically conditioned nictitating membrane response (NM CR) of rabbit, a widely used model system for studies of learning. One experimental approach involved recording from single brain neurons from awake, behaving animals for the purpose of determining the loci and characteristics of neurons with activity correlated with the NM CR or its inhibition. A second approach involved the use of discrete brain lesions that selectively eliminate the NM CR while at the same time sparing the basic reflex pathway. A third approach employed fiber-tracing anatomical techniques designed to clarify the interconnectivity among brain regions essential for the NM CR. These regions include discrete portions of the cerebellum and brain stem. Information from physiological studies has been incorporated into mathematical models of learning used by adaptive network researchers, and anatomical findings have guided the development of related neuronal

models.

II Research Objectives

A. Overview The project's primary objective was to conduct neurobiological studies relevant to adaptive networks using the classically conditioned nictitating membrane (NM) response as a model system. The classically conditioned NM response (NM CR) in rabbit has been widely adopted as a model system for behavioral, neurobiological, and theoretical studies of mammalian associative learning. Previous reports might be consulted in the interest of continuity. The Research Progress and Forecast Report dated 11/27/84, for example, contains a good deal of information detailing the rationale for our theoretical and experimetal work during the reporting period. That report describes some relevant scientific interactions that are only briefly noted here.

It is generally held that many brain regions contribute to learning the NM CR and that these regions interact with each other via pathways that parallel the basic reflex pathway underlying the unconditioned response (UR). Neural circuits responsible for the CR converge, on the response side, among motoneuron pools that retract the eyeball, principally the accessory abducens nucleus (AAN). On the stimulus side, rostral elements of the sensory trigeminal complex subserve the unconditioned stimulus (US). A comparatively simple disynaptic reflex arc completes the circuit between stimulation of the eye and defensive retraction of the globe. NM extension is a passive consequence of eyeball retraction. Circuits mediating the NM CR include discrete portions of the cerebellum and reticular information. These systems appear to interact with other brain regions that modulate the rate of CR acquisition, CR topography, and inhibition; they include the septo-hippocampal complex and poorly differentiated regions of the midbrain.

Behavioral/biological studies of learning using the rabbit NM preparation have implications for adaptive network research because they can guide and validate assumptions underlying mathematical models learning. Promising models suggest algorithms that are potentially applicable to problems of artificial or machine learning. In addition, by successfully modelling the fine-grain topographical features of the learned response in real time, our efforts would appear relevant to problems of sensory motor control in two domains: physiology and robotics.

We were particularly interested in the model described in 1981 by Drs. R.S. Sutton and A.G. Barto of the Department of Computer and Information Sciences in connection with their studies of adaptive networks (R.S. Sutton & A.G. Barto, Toward a modern theory of adaptive networks: Expectation and prediction. Psychological Review, 1981, 88, 135-170). Our group, primarily John E.Desmond, Dr. N.E. Berthier, Diana Blazis, and myself, have developed real-time variants of this model capable of predicting patterns of neuronal firing and CR topography (latency, amplitude, and form) typically observed in the rabbit NM preparation. The model has validity for a variety paradigms and training protocols. This effort profited from interactions with Barto and Sutton and other experts in relevant behavioral domains, principally E. J. Kehoe and my colleague J. J. B. Ayres. In a related line of work, Nestor Schmajuk and I developed attentional models of associative learning, derived from psychology, into computational adaptive networks capable, not only describing neural correlates of learned behavior and CR topography in real time, but also of describing the contribution of the hippocampal formation to the NM CR and perhaps other instances of learning.

B. Purpose of Specific Studies Specific studies during the reporting period fall into four main categories: electrophysiological, anatomical, lesions, and theoretical.

1. Electrophysiological Briefly, our physiological studies involved single or multiple-unit extracellular recording from brains of awake, behaving animals. We now rely exclusively on single-unit methodology. Their purpose was to determine the precise loci and firing pattern of neurons with activity related to the CR or its inhibition. This information is crucial for understanding, not only which brain regions and structures are involved in a particular aspect of the CR, but how these regions and structures interact to perform their designated tasks. Neuronal representations of these processes in the form of connectionistic schemas can be viewed as models of parallel cooperative computation. During the period of the current grant, and with funds provided by NSF and NIH in addition to AFOSR, we have constructed three complete computer-assisted laboratory for single-unit neuronal recording concurrent with behavioral testing for the purpose of investigating the relationship between neuronal activity and the NM CR. One laboratory is used by Neil E. Berthier, another by John E. Desmond, and the third by William G. Richards. These three individuals are postdoctoral associates/fellows. Prior to the current grant, my laboratory was limited to one electrophysiology setup, and that was only capable of multiple-unit recording.

Electrophysiological studies completed over the grant period include two doctoral dissertation projects, one of which has been completed and the Ph.D. degree awarded (John E. Desmond) and the other of which is still being written up by the candidate (Michael Vigorito). In terms of publications involving neuronal recording, one paper (Berthier & Moore, 1986) is "in press" in Experiental Brain Research and another (Desmond & Moore, 1986) has been accepted by that journal pending revisions. Results of these studies have also been presented at several meetings as invited talks or poster presentations.

2. Anatomical Anatomical studies addressed the interconnectivity of brain structures essential for the NM CR, especially the anatomical relationships among the accessory abducen nucleus (AAN), the principal source of motor control the NM CR, and magnocellular red nucleus (RN), an essential premotor link in the circuit. We used implanted WGA-HRP for fiber tracing studies designed to verify our previously reported findings with HRP that RN projects to AAN. We were also concerned about brain stem projections to AAN from the dorsolateral pons and cerebellum. This research is in its final stages: a report earmarked for publication is being prepared at this time, and an abstract for presentation of our findings at the next Society for Neurosciences meeting has been submitted. Basically, our findings with WGA-HRP are entirely consistent with our previously published results based on HRP.

During the past 12 months we initiated another WGA-HRP study designed specifically to detect the existence in rabbit of an ipsilateral descending limb of brachium conjunctivum (BC) terminating in the dorsolateral pons. As a possible premotor component of the NM CR, such an anatomical entity might account for CR-related single neuron activity observed in the dorsolateral pons and reported by Desmond and Moore. Despite reports of such a descending limb of BC in rat and monkey based on autoradiographic methods, we have thus far been unable to detect a homologuous projection system in rabbit. These results will also be presented this fall at the Society for Neuroscience meetings.

Anatomical studies such as these made use of a powerful light microscopy system purchased with funds provided by a DoD instrumentation grant (AFOSR 85 0079).

3. Lesion Studies These studies addressed the question of brain regions/structures essential for the NM CR and its inhibition. Three completed and published studies document the fact that red nucleus (RN) is an essential premotor component of the NM CR. Lesion experiments designed to locate brain systems essential for inhibition of the NM CR, mentioned in prior technical reports, have been suspended for lack of conclusive evidence. Simply put, the project was not yielding sufficiently clear cut evidence in relation to the time and effort required by experimenters. Forebrain systems that seemed promising candidates base on preliminary data, e.g., lateral septal nuclei, have not in fact proven to be crucial for learned inhibition of the NM CR. We are in no hurry to publish our rather sizable accumulation of negative evidence.

4. Theoretical As mentioned above, this aspect of our activity used data on the NM CR from behavioral and physiological domains to guide formulation of computational models of learning and assess their validity. One class of models under scrutiny are constrained variants of the original Sutton-Barto (S-B) model consisting of a single adaptive

element. A paper describing a variant of the S-B model suitable for real-time intratrial features of the NM CR and associated neural activity is in press in Behavioural Brain Research , and the work will be presented this summer at the Cognitive Science Society meetings. A related theoretical approach to intratrial descriptions of conditioning phenomena was developed by John Desmond will be presented at the next Society for Neuroscience meetings. A third class of models, derived from attentional theories of learning and incorporating a role for the hippocampus, has also been studied through simulation experiments. This line of research has culmintad in a successful Ph.D. dissertation by Nestor Schmajuk, one published report in Physiological Psychology , a manuscript that has been submitted to Psychological Review , and a paper that will shortly be submitted to The Journal of Experimental Psychology: Animal Behavior Processes.

Over the past year we have worked closely with other theorists doing related work on conditioning: A. H. Klopf, R. S. Sutton, E. J. Kehoe, and J. J. B. Ayres. In addition, a graduate seminar offerred by me during the past semester was largely devoted to theoretical issues bearing on learning algorithms of interest to adaptive network researchers. Although intended for students, the seminar also attracted the participation of several colleagues.

III Status of Research

A. Electrophysiological Studies

1. Analysis of learning related single neurons of the brain stem This was John Desmond's dissertation project. Extracellular recording from single neurons were obtained during behavioral training.

Most sampled units were located in pontine reticular formation. The relationship between unit firing patterns and topographical features of the CR was investigated with an impressive array of quantitive tools developed by Desmond, including multiple regression, peristimulus and periresponse histograms, and time-correlograms. Such analyses aided development computational models models of learning related neuronal activity.

Two main types of CR-related neuronal activity were observed. On-cells increase their activity so as to mirror aspects of CR topography such as latency and amplitude. These neurons form a template of the CR as much as 100 msec before the CR begins. Such neurons are either causally related to the CR or else they reflect processing and representation within a parallel system, as portrayed in previously published neuronal models. A subset of neurons with CR-related activity decrease their firing rates in relation to the NM CR. Desmond's dissertation has been duplicated as a technical report entitled "The classically conditioned nictitating membrane response: Analysis of learning-related single neurons of the brain stem", Sept. 1985.

2. Multiple-unit correlates of conditioned inhibition This study is Michael Vigorito's dissertation project. Its methodology resembles that employed in the Desmond study, except that multiple-unit recordings were the rule and single units an exception. Certain theoretical models assume that CI develops in a distinct system that parallels those involved in CR acquisition. Inhibition of a CR presumably arises because of interactions between these two systems at some as yet unknown premotor stage. In this connection it is interesting that a neuronal interpretation of the S-B model does not

require a separate system in order to generate CI. Thus, the S-B model cannot be construed as an accurate representation of how CI emerges in real brains. Nevertheless, a good deal of our simulation work with S-B model concerns scenarios that lead to the development of CI (or negative "synaptic weights" in the model's argot). The model makes interesting and testable predictions about CI in scenarios for which there is as yet no relevant data.

Recording from brain regions now thought to be important for conditioned inhibition, but not for acquisition or generation of the NM CR, Vigorito observed neurons that increased their firing rate as the CR was actively suppressed in the presence of a conditioned inhibitor. Units of this type were observed in lateral septal nuclei, lateral habenula, and ventromedial thalamus. By contrast, units that increase their firing in the absence of CRs were not observed in Desmond's study. Vigorito left this laboratory in 1984 to pursue professional opportunities elsewhere. Due to a variety of personal (family) problems and his other profession commitments in research and yeaching, he has not yet completed his dissertation. He has indicated that this will been done this summer, as he has taken leave from his present positions.

3. <u>Single-unit recording from cerebellar Purkinje cells</u> Neil Berthier conducted studies showing that hemispheric lobule VI of cerebellar cortex contains Purkinje cells with activity related to the NM CR. Lesion studies have shown that hemispheric lobule VI is essential for the NM CR. As indicated above a complete desription of this work to date will appear soon in <u>Experimental Brain Research</u> . For this reason I have omitted a detailed summary of our findings here.

B. <u>Anatomical Studies</u>

Studies of the interconnectivity among brain regions implicated in the NM CR were conducted using WGA-HRP (TMB) as a marker. Because unilateral lesions of magnocellular red nucleus (RN) and its projections eliminate the NM CR on the side opposite to the lesion, we used WGA-HRP to determine the trajectory of two of the primary input/output fiber systems to RN: the brachium conjunctivum (BC), which conveys information from anterior nucleus interpositus of the contralateral cerebellar hemisphere; the rubrobulbar tact, which carries information from red nucleus to the region of AAN on contralateral side of the brain stem. A preliminary description of this work has been published in Physiology & Behavior. The principal contribution to the CR from RN to AAN is by way of interneurons in the spinal trigeminal complex. Thus, it now appears that RN exerts the greatest part of its control over the NM CR by exciting a secondary sensory component of the reflex pathway rather than by exciting AAN directly. Nevertheless, WGA-HRP material confirms the existence of a sparse direct projection from large RN cells of the dorso-medial portion of RN to AAN, as described in a previously published HRP study from this laboratory.

As mentioned above, we have been using WGA-HRP to detect possible ipsilateral projections from cerebellar nuclei interpositus and dentate to brain stem regions implicated in NM conditioning by Desmond's research. According to reports with rats and monkeys, such ipsilateral projections (the descending limb of BC) are more likely to involve the dentate rather than interpositus deep nucleus. We implanted WGA-HRP in relevant regions of the pons and examined dentate and interpositus for retrograde labelling of neuronal somas. In addition, we implanted the marker into deep nuclear zones and examined the pons for terminals in the regions of interest. We have no clear evidence that dentate/interpositus neurons make direct ipsilateral to pontine regions implicated by Desmond. This negative evidence supports our hypothesis that the essential premotor control of the NM CR exerted by the cerebellum cannot account for Desmond's results, and that the dorsolateral pons participates in generation of CR as a logical AND GATE. That is, two seperate neural circuits are essential for expression of the CR; one involves the cerebellum, and the other involves the pontine reticular formation. The two circuits both receive CS and US information, but they only converge at the level of motoneurons (and their immediate afferents of the sensory trigeminal complex) associated with the abducens nerve. Stated somewhat differently, because as their repective components are not interconnected monosynaptically, neither circuit can be regarded simply as a slave of the other. The processing of CS-US information necessary for learning evidentally occurs in parallel.

We are undecided regarding suitable venues for publication of anatomical studies conducted over the period of the grant. The study focusing premarily on the relationship between RN and AAN would be perhaps best suited for Brain Research Bulletin because this is where our initial study on this subject appeared. That journal was selected because of its superior reproduction of anatomical material and emphasis on behavioral neuroscience. The study on the descending limb of BC, however, will probably be submitted to Experimental Brain Research because this journal has become a highly visible outlet for quality work on rabbit NM conditioning, and it is the journal in which some of the evidence for a descending limb of BC has been published.

C. Lesion Studies

1. Lesions of brachium conjunctivum and rubrobulbar tract eliminate the NM CR. As noted above, unilateral lesions of these two fibers systems eliminate the NM CR but not the UR. Other lesions of the dorsolateral pons caudal to the abducens nerve have no effect on behavior. This study, which was conducted by technician Marcy Rosenfield, reinforced our earlier conclusion that the supratrigeminal reticular formation, like the cerebellum, is essential for the NM CR. A description of this work has been published in Physiology & Behavior.

2. Bilateral lesions of hypothalamus do not impair conditioned inhibition. Diana Blazis, a graduate student in my laboratory since 9/84, conducted this study as an undergraduate honors thesis. A variety of theoretical considerations, together with earlier lesion studies by Moore and his collaborators here and in London, suggested the possibility of hypothalamic involvement in CI. Blazis' study does not support this hypothesis. The histological material suggested that the lateral septal area and habenula may be involved in CI. This hypothesis would be consistent with Vigorito's recording study and earlier lesion studies from this laboratory involving the midbrain. Blazis and Rosenfield initiated lesion studies based on these leads. They investigated effects of septal area lesions on CI and began to extend these studies to the habenula. However, because the relationship between lesions of these brain regions and disruption of CI was these regions and CI was less than clearcut, I suspended this line of research pending completion of Vigorito's dissertation.

3. Lesions that disrupt the NM CR do not affect the UR. From a variety of theoretical perspectives, the extent to which lesions that

disrupt the CRs might also influence the UR is an important issue. For example, certain neuronal models suggest that CR-disrupting lesions should produce a slight, but nevertheless significant, attentuation of the UR over a range of intensities of the eliciting stimulus. This does not appear to be the case. Our researchs were presented at the 1984 Society for Neuroscience meetings and in a paper by Rosenfield and myself that appeared in Behavioral Brain Research.

D. Theoretical Studies

1. Physiologically constrained Sutton-Barto learning models. Literally hundreds of simulations experiments were conducted in efforts to discover variants of the S-B model that are most consistent with behavioral data on the NM CR. This work has been largely successful, and published descriptions will appear in Behavioural Brain Research , Proceedings of the Cognitive Science Society meetings of 1986. A preliminary report of this work was presented at the 1985 meetings of that society. Diana Blazis has been assessing a number of elaborations of the model designed to enhance its ability to describe NM conditioning data at the intra- and intertrial levels.

2. Physiologically constrained attentional models This is basically Nestor Schmajuk's dissertation project, which was successfully completed this past semester. He and I performed hundreds of simulation studies and prepared three papers for publication, as indicated above.

3. John Desmond has developed a two-element neuronal network model and set of algoritms that appears to to be a considerable advance on the basic one-element S-B model. Desmond's model is applicable to a problem that has not been addressed by any other model, namely, the problem of describing and simulating the real-time topography of the CR

that results when animals (or people, for that matter) are trained under conditions in which the time between the onset a CS and the onset of the US varies from one trial to the next. Algoritms like Desmond's that acquire adaptive motor programs when the timing between two events varies may prove useful in the domains of AI and motor control. My colleague A. G. Barto believes Desmond's approach may be applicable to problems of motor control in speech, a project he is working on with his post-doctoral research associate Michael Jordan. Desmond's work will be presented at the meetings of the Society for Neuroscience this fall.

IV Technical Reports (Publications)

1. Moore, J.W. & Solomon, P.R. Forebrain-brain stem interaction: conditioning and the hippocampus. In L. Squire & N. Butters (Eds.) Neuropsychology of memory. New York: Guilford, 1984, pp. 462-472.

2. Moore, J.W. & Stickney, K.J. Antiassociations: Conditioned inhibition in attentional-associative networks. In R.R. Miller & N.E. Spear (Eds.) Information processing in animals: Conditioned inhibition. Hillsdale, N.J.: Erlbaum, 1985, pp. 209-232.

3. Berthier, N.E. The role of extraocular muscles in the rabbit nictitating membrane response: a reexamination. Behavioural Brain Research, 1984, 14, 81-84.

4. Rosenfield, M.E., Dovydaitis, A., & Moore, J.W. Brachium conjunctivum and rubrobulbar tract: Brain stem projections of red nucleus essential for the conditioned nictitating membrane response. Physiology & Behavior, 1985, 34, 761-768.

5. Rosenfield, M.E. & Moore, J.W. Red nucleus lesions impair acquisition of the classically conditioned nictitating membrane response

but not eye-to-eye savings or UR amplitude. Behavioral_Brain_Research, 1985, 17, 77-81.

6. Schmajuk, N.A. & Moore, J.W. Real-time attentional models for classical conditioning and the hippocampus. Physiological_Psychology, 1985, 13, 278-290.

7. Moore, J.W., Desmond, J.E., Berthier, N.E., Blazis, D.E.J., Sutton, R.S., & Barto, A.G. Connectionistic learning in real time: Sutton-Barto adaptive element and classical condition of the nictitating membrane response. Proceedings_of_the_Seventh_Annual_Conference_of_The Cognitive_Science_Society, 1985, 318-322.

8. Moore, J.W. Two model systems. In Alkon, D.L. & Woody, C.D. (Eds.) Neural_mechanisms_of_conditioning. New York: Plenum, 1985, 209-219.

9. Berthier, N.E. & Moore, J.W. Cerebellar Purkinje cell activity related to the classically conditioned nictitating membrane response. Experimental_Brain_Research, In press.

10. Moore, J.W., Desmond, J.E., Berthier, N.E., Blazis, D.E.J., Sutton, R.S., & Barto, A.G. Simulation of the classically conditioned nictitating membrane response by as neuron-like adaptive element: Response topography, neuronal firing, and interstimulus intervals. Behavioural_Brain_Research, In press.

11. Desmond, J.E. & Moore, J.W. Dorsolateral pontine tegmentum and the classically conditioned nictitating membrane response: Analysis of CR-related single-unit activity. Experimental_Brain_Research, Accepted pending revisions.

V Professional_Personnel

1. John W.Moore, Ph.D., Professor of Psychology (Neuroscience Behavior) and Associated Professor of Computer and Information Sciences.

2. Neil E.Berthier, Ph.D., Research Associate.

3. John E. Desmond, Ph.D., Research Associate. Dr. Desmond pursued his Ph.D. in this laboratory and the degree was awarded Sept., 1985. His dissertation is entitled "The Classically Conditioned Nictitating Membrane Response: Analysis of Learning-Related Single Neurons of the Brain Stem." Desmond presented his findings at the 1985 meetings of the Society for Neuroscience and the Psychonomic Society.

4. Nestor A. Schmajuk, Ph.D., who is presently at the Boston University Center for Adaptive Systems, pursued his Ph.D. in this laboratory. The degree was awarded May, 1986. His dissertation is entitled "Real-Time Attentional Models for the Classically Conditioned Nictitating Membrane Response."

5. William G. Richards, Ph.D., NIH post-doctoral fellow.

VI Interactions

A. Formal Presentations by Moore during Year Three

1. Invited lecture entitled "Purkinje cell activity related to the conditioned nictitating membrane response". Second Biennial Symposium on Neural Mechanisms of Conditioning, King's College, Cambridge (U.K.), Sept. 16-18, 1985.

2. Principal participant at Fourth Winter Conference on Animal Learning, Winter Park, Colorado, Jan. 18-21, 1986.

3. Invited participant at Tenth Winter Conference on Neurobiology of Learning and Memory, Park City, Utah, Jan. 11-14, 1986.

4. Invited lecture entitled "Purkinje cell activity during NMR

conditioning". NATO ARW Workshop Conference on Cerebellum and Neuronal Plasticity, Magdalen College, Oxford (U.K.), April 7-9, 1986. A chapter will be published with the proceedings of this workshop under the title "Cerebellar and Brain Stem Substrates of the Classically Conditioned Nictitating Membrane Response".

5. Colloquium entitled "Brain Substrates of Conditioned Response Learning". University of Alabama, Birmingham, Alabama, Oct. 1, 1985.

6. Peer reviewed poster presentation at the Seventh Annual Conference of the Cognitive Science Society, Irvine, California, Aug. 15-17, 1985.

B. Formal collaboration

1. Douglas Coulter, working in Daniel Alkon's laboratory at Marine Biological Laboratory, Woods Hole, Mass., and John Disterhoft of Northwestern University are investigating biophysical properties of hippocampal pyramidal cells in slices from rabbits that had NM CR training. In 2/85, I provided the apparatus they are now using for the training phases of these experiments. The collaboration has resulted in a coauthored paper to be presented at the 1985 meetings of the Society for Neuroscience. A technical report of this work is being prepared at this time.

2. Dr. E.J. Kehoe, Ph.D., of the University of New South Wales, Australia, is collaborating with us on experiments designed to test strong predictions of various learning algorithms derived from the Sutton-Barto model.

C. Informal collaborations

1. We remain in close contact with Dr. C. H. Yeo and his London collaborators concerning neural substrates of the NM CR.

2. Our interactions with Dr. A. G. Barto and with group, including Richard Sutton, now at GTE in Waltham, Mass., continue. The three of us visited Dr. A.H. Klopf at WPAFB for approximately two days this past Feb. in order to discuss theories of classical conditioning and more complex forms of learning. A good deal of time was devoted to experiments using Dr. Klopf's simulator. John Desmond, Diana Blazis and I visited Dr. Klopf in June of this year for the same purpose.

VII <u>New Discoveries</u>

The primary new discovery during the reporting period concern CR- related single unit activity in brain stem and cerebellar cortex. The demonstration of CR-related single-unit activity in cerebellar Purkinje cells is particularly noteworthy because it supports theories of cerebellar learning of Marr-Albus. Also noteworthy is our failure to find anatomical evidence for an ipsilateral descending limb of BC.

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